

A NEW SPECIES OF *GIGANTODAX* ENDERLEIN (DIPTERA: SIMULIIDAE)
FROM THE UNITED STATES

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Abstract.—The larva, pupa, and adults of *Gigantodax adleri*, new species, are described from small springs in eastern Arizona and western New Mexico. This species represents the first United States record for the genus and a northern range extension of more than 3000 km. The preimaginal stages are associated with those of two species, *Simulium patziciaense* Takaoka and Takahasi and *Simulium puigi* Vargas, Martínez Palacios, and Díaz Nájera, not previously recorded north of Guatemala and southern Mexico, respectively. *Gigantodax adleri* belongs to the *Gigantodax wrighti* group of Wygodzinsky and Coscarón, and its life stages are superficially similar to those of several congeneric species. Diagnoses that differentiate the female, male, and pupa from those of all other species and a detailed description of the preimaginal habitat are provided.

Key Words: North America, springs, aquatic insect, Nematocera

Gigantodax Enderlein, with 67 currently recognized species, is the third largest black fly genus and the second largest in the southern hemisphere. Typically, it is placed within the Prosimuliini, which along with the Simuliini comprise the Simuliinae (Wygodzinsky and Coscarón 1973, 1989, Crosskey 1988, Takaoka et al. 1988, Vargas and Ramírez-Pérez 1989). Currie (1988), however, redefined the tribal limits within the Simuliinae and restricted the Prosimuliini to include only the following genera: *Prosimulium* Roubaud, *Helodon* Enderlein, *Urosimulium* Contini, *Levitinia* Chubareva and Petrova, *Gymnopais* Stone, and *Twinnia* Stone and Jamnback. As a result, *Gigantodax* and the remaining genera within the Simuliinae were assigned to the Simuliini, a view that is also corroborated by DNA sequence data (J. K. Moulton, unpublished).

Larvae of *Gigantodax* are the only ones in the family with a seventeen-toothed hypostoma, a complete, well sclerotized ring

around the anal proleg, and posteroventrally directed struts underlying the base of the dorsal arms of the anal sclerite (Wygodzinsky and Coscarón 1989). The pupae are best known for their spectacular diversity in gill structure, which alone will separate many species. Some species, however, possess more typical gills and are scarcely separable from those of other genera. The adults are easily recognized by the straight, rather than sinuous, CuA_2 vein and the distinctive terminalia. The terminalia, however, are indistinguishable from those of species in the genus *Cnesia* Enderlein, which is its sister group (Wygodzinsky and Coscarón 1973, 1989).

The greatest diversity in this genus occurs in the Andes, but representatives of the *G. wrighti* species-group (Wygodzinsky and Coscarón 1989) are known as far north as the Sierra Madre de Occidental of central Mexico (Dalmat 1955, Vargas and Díaz Nájera 1957, Wygodzinsky and Coscarón

1989). Larval habitats range from small springs and rivulets to medium-sized rivers, and some species are found only in acidic or alkaline watercourses (Dalmat 1955, Wygodzinsky and Coscarón 1989). Females are presumably ornithophilic based upon the large basal tooth of the tarsal claw (Shewell 1955).

Wygodzinsky and Coscarón (1989) recognized eight species groups within *Gigantodax*, the *G. brophyi*, *G. cilicinus*, *G. cornonsi*, *G. cortesi*, *G. igniculus*, *G. minor*, *G. multifilis*, and *G. wrighti* groups, which contained 17, 11, 10, 4, 2, 4, 1, and 15 species, respectively, at that time. Since their treatise, three additional species have been described (Takaoka et al. 1988, Vargas and Ramírez-Pérez 1989). *Gigantodax biergi* and *G. williei*, described from Costa Rica by Vargas and Ramírez-Pérez (1989), belong to the *G. wrighti* group, and *Gigantodax lazoii*, described from Ecuador by Takaoka et al. (1988), is assignable to the *G. cornonsi* group.

In this paper, all life stages, after the egg, are described for a new species of black fly in the *G. wrighti* species group that represents the northernmost record for the genus and a new generic record for the United States. Also provided are diagnoses that differentiate the pupa and adults from those of all other species in the genus and a detailed account of the preimaginal habitat. The description below provides a name for this species that will enable its inclusion in a book on the black flies of North America being prepared by P. H. Adler, D. C. Currie, and D. M. Wood.

MATERIALS AND METHODS

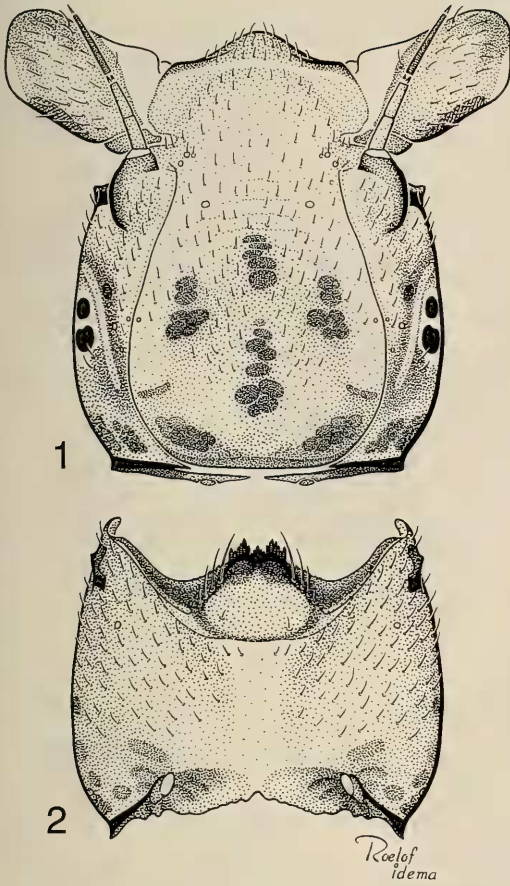
Life-stage descriptions largely follow that of Adler and Currie (1986). Taxonomic terms predominantly follow that of Peterson (1981). Representative larvae were preserved in absolute ethanol or Carnoy's fixative, while others were transported live to the laboratory and reared in water taken from the type locality and maintained at 10°C. All but one of the pupae and one of

the two males were obtained from these rearings. The majority of adults were collected over the course of three days using an emergence trap placed directly above an exposed portion of the spring. The adults were placed into 95% ethanol immediately upon their discovery in the net. Paratype larvae, deposited in collections other than the author's, that were initially fixed in Carnoy's solution were transferred to 80% ethanol for permanent storage. Pupae were preserved in 60% ethanol to prevent collapsing of the gills, and then transferred to 80% ethanol for permanent storage. The holotype and all pinned adults were dehydrated with absolute ethanol and dried using hexamethyldisilazane, HMDS (Polysciences, Inc.). The holotype and some paratypes are deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM). Additional paratypes are deposited in the Canadian National Collection, Ottawa (CNC), The Natural History Museum, London (NHM), the American Museum of Natural History, New York (AMNH), and the author's personal collection (JKM). The figures of the larval head capsule, pupa, and male and female terminalia were drawn by Ralph Idema for the upcoming book on the black flies of North America and were made available to me by D. M. Wood. The remaining drawings were rendered by the author with the aid of an MTI CCD72 imaging system connected to an Olympus SZH10 stereo microscope. Length and width measurements were made using either this imaging system or by an ocular micrometer in an Olympus SZH zoom stereo microscope. Terminalia, mouthparts, and legs were cleared in 85% lactic acid to facilitate visibility and interpretation.

DESCRIPTION

Gigantodax adleri Moulton, new species (Figs. 1–17)

Larva (mature).—Length 6.9–7.2 mm ($x = 7.0$, $n = 5$). General color of larva pink-

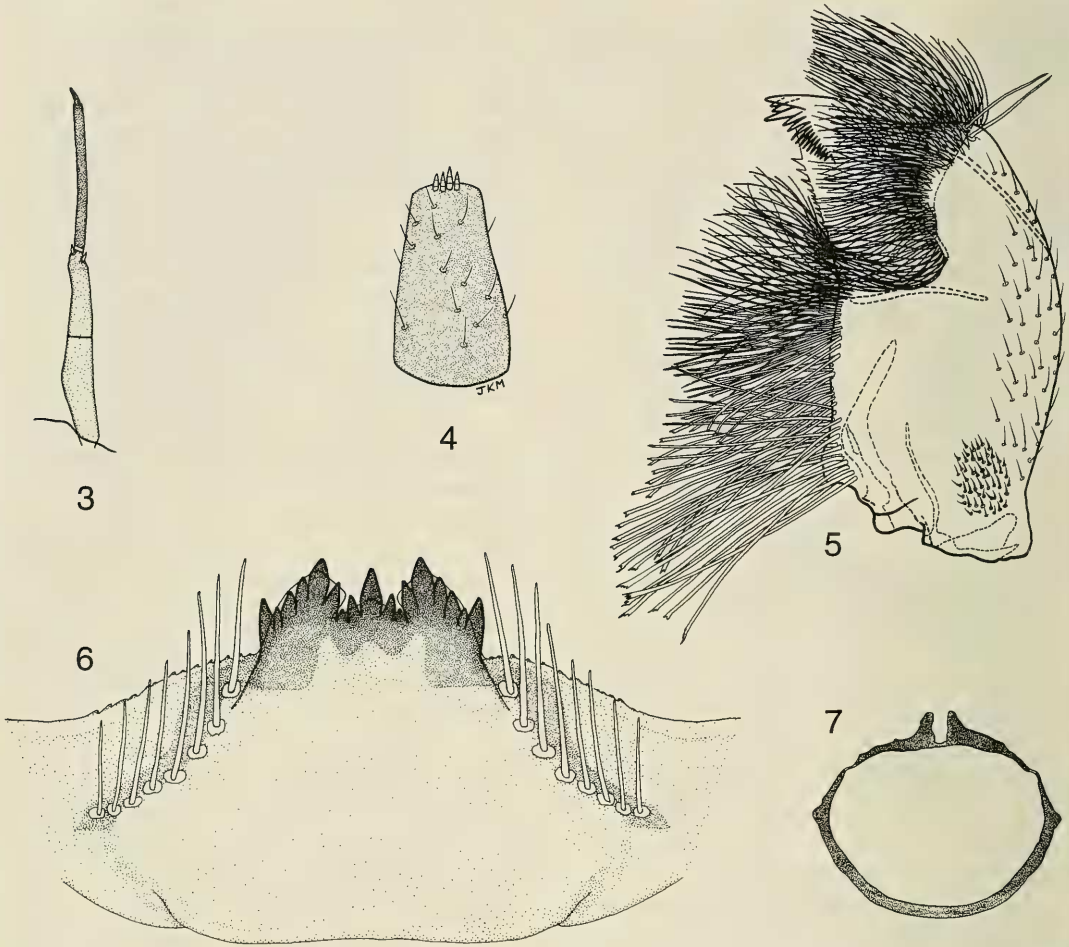


Figs. 1–2. *Gigantodax adleri*. 1, Larval head capsule (dorsal view). 2, Larval head capsule (ventral view).

ish beige to brown; intersegmental bands poorly defined. Head capsule (Figs. 1, 2) extremely variable in color, ranging from pale yellowish brown with distinct, dark-brown headspots (pinkish beige larvae) to brown with headspots only slightly darker brown than background and rather indistinct (brown larvae). Headspots subequal in intensity and clearly comprised of multiple smaller spots; anterior posterolateral spot very small and concave; line over eyespots thin, brown, and with small oval spot positioned anterior of midlength. Antenna (Fig. 3) shorter than stem of labral fan, somewhat pigmented, with apical article darker than basal two; proportions of articles (distal to proximal) 1.4:1.0:2.3; termi-

nal sensillum 3.4 times longer than basal width. Labral fan with 24–31 primary rays ($x = 28$, $n = 4$). Maxillary palpus (Fig. 4) about 1.9 times longer than basal width. Mandible (Fig. 5) with 10–11 inner teeth and 9–10 marginal serrations. Hypostomal bridge slightly darker than remainder of undersurface of head capsule, with faintly perceptible median longitudinal, light-colored stripe. Hypostoma (Fig. 6) with 17 teeth, one median tooth and 8 others per side; median tooth shorter than tallest lateral tooth; first tooth from median arising outwardly from near the base of median tooth; second tooth from median deeply set and barely surpassing dorsal wall; third tooth from median about as tall as median tooth; fourth tooth from median tallest tooth, its apex sloped outwardly; fifth and sixth teeth from median subequal in size although arising along downward slope; seventh tooth from median smallest of outer group of 5 teeth; eighth tooth from median prominent, its apex directed slightly inwardly. Lateral margin of hypostoma with 5–6 hypostomal setae and 7–8 lateral serrations per side. Postgenal cleft nearly imperceptible, at most a small notch. Cervical sclerites partially enclosed anteriorly by arms of postociput. Thoracic proleg with lateral plate subquadrate, moderately sclerotized. Perianal scales not developed. Ventral papillae small, but distinct. Anal sclerite X-shaped, with heavily sclerotized, posteroventrally directed struts arising from base of anterior arms; posterior arms continuous as a well-sclerotized, thin, brown ring (Fig. 7) surrounding posterior proleg. Posterior proleg with approximately 135 rows, each with 20–27 hooks. Anal papillae of three simple lobes.

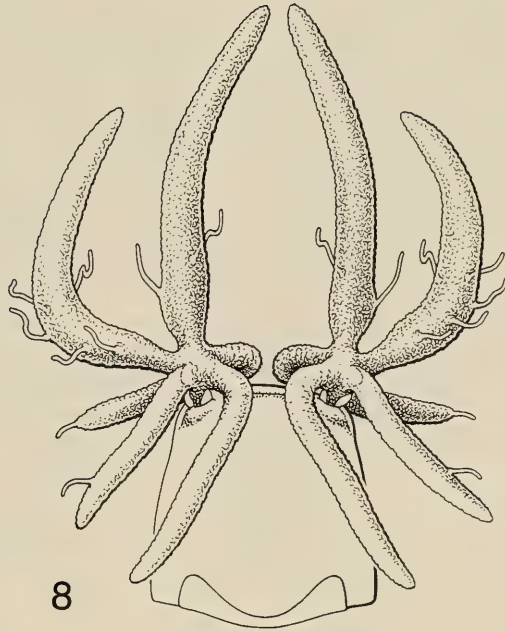
Pupa (Figs. 8–9).—Length of pupal body = 3.2–3.5 mm ($x = 3.3$, $n = 5$). Antenna sheath of female extended slightly beyond posterior margin of head; antennal sheath of male extended about 2/3 distance to posterior margin of head. Frontoclypeus of both sexes of normal shape, except for square protuberance medially, and with numerous



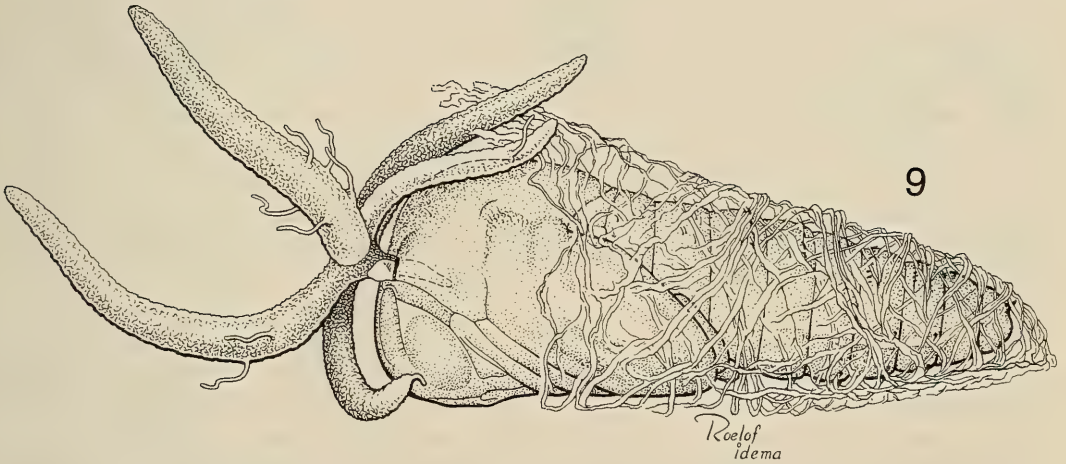
Figs. 3-7. *Gigantodax adleri*. 3, Larval antenna. 4, Larval maxillary palpus. 5, Left larval mandible (ventral view). 6, Larval hypostoma. 7, Larval anal salerite (terminal view).

regularly spaced, lightly verrucose platelets. Frontal and clypeal trichomes in the form of strong setae. Gill about $2/5$ - $1/2$ length of pupa, comprised of five, flimsy, pale gray, corrugated, tubular filaments arising individually from a short, common base; two dorsal branches directed posteriorly, two median branches directed anterodorsally, and a ventral branch directed posteriorly; dorsal branches simple or with one terminal or subterminal filament; median branches slightly thicker than others, the dorsalmost one with 4-5 and the other with 1-2 short, somewhat coiled filaments positioned just basal to midlength; ventral branch usually

with one short apical filament. Thorax with numerous, rather regularly spaced, slightly verrucose platelets. Dorsocentral and dorsolateral trichomes setalike. Abdomen with platelets dorsally. Abdominal chaetotaxy as follows: tergite I with 4 setae per side; tergite II with 6-7 setae per side; tergites III and IV each with 4 retrorse hooks and 3 setae per side, one setae anterior to fourth hook from midline and 2 setae laterally; tergite V with 3 setae per side; tergites VI and VII with anterior row of spine combs and 1 seta per side; tergite VIII with anterior row of spine combs and 2-3 setae per side; tergite IX with pair of strong terminal



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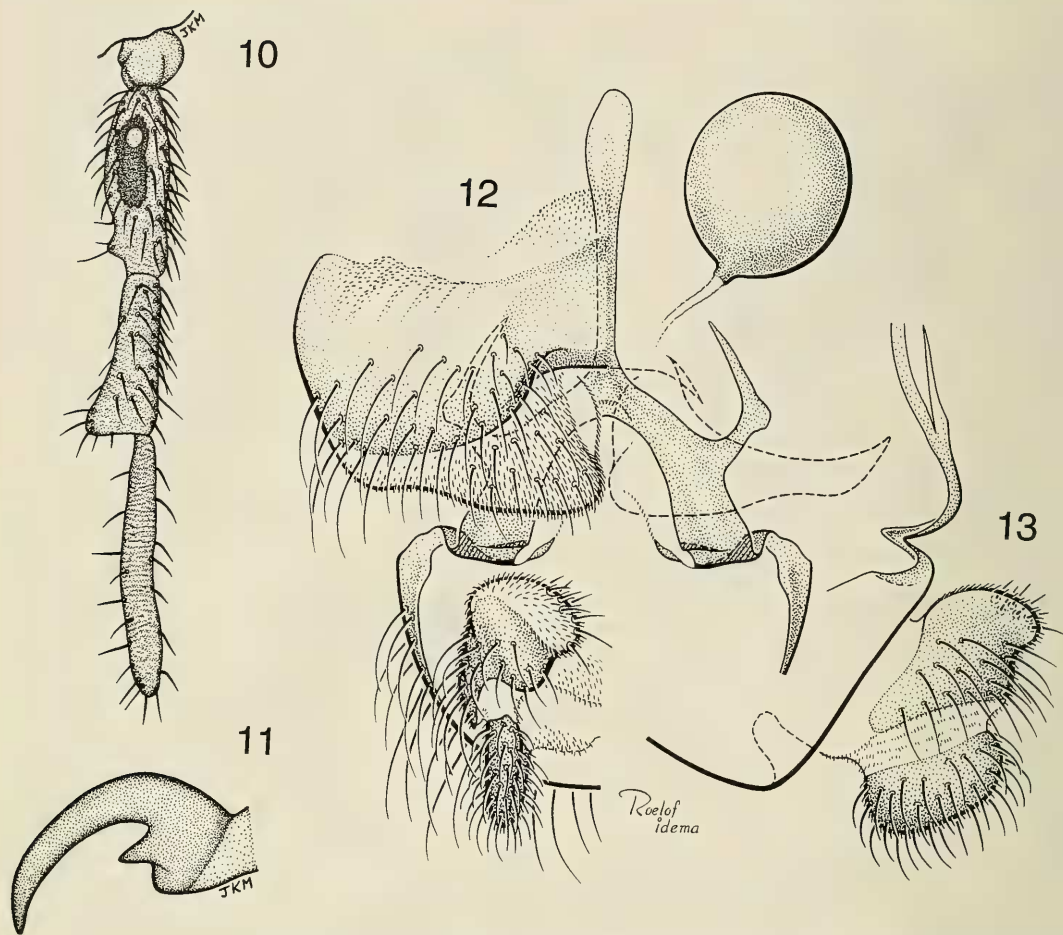
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Figs. 8-9. *Gigantodax adleri*. 8, Pupal thorax and gills (dorsal view). 9, Pupa and cocoon (lateral view).

hooks and 2 setae per side. Sternite IV with 2 setae per side, situated medially; sternite V with 3 evenly spaced hook-like setae per side; sternite VI divided medially, each half with 2 short, grapple-like hooks; sternite VII divided medially, each half with 1 grapple-like hook; each half of sternites VI and VII bears a pleural sclerite with 1 grapple-like hook; sternite VIII glabrous; sternite IX

with 3 long setae per side. Cocoon pale brown, covering abdomen and posterior portion of thorax, and often encrusted with small organic and inorganic particles.

Female.—General body color bright orange with golden pile. Length: thorax 1.2–1.4 ($x = 1.3$, $n = 4$) mm; wing 3.4–4.4 ($x = 4.0$, $n = 4$) mm. Frons gray, at vertex about 3 times broader than at narrowest



Figs. 10–13. *Gigantodax adleri*. 10, Female left maxillary palpus (dorsal view). 11, Female tarsal claw (lateral view). 12, Female terminalia (ventral view with left anal lobe and cercus removed). 13, Female right anal lobe and cercus (lateral view).

point, with sparse golden pile. Frontal angle 77° . Fronto-ocular triangle about as high as wide. Clypeus brown, about as long as wide, with golden pile. Occiput gray, with golden pile reaching posterior margin of eye; postocular setae golden. Antenna with brown pile; scape and pedicel orange; flagellum orange, with apical two flagellomeres slightly darker. Proboscis brown. Mandible with 20 teeth along inner margin. Lacinia with 18 retrorse teeth. Palpus brown, with stout brown setae; ratio of palpomeres (Fig. 10) 1.2:1.0:1.6; sensory vesicle of palpomere III elongate, about 0.6 times length of segment, with external opening rounded

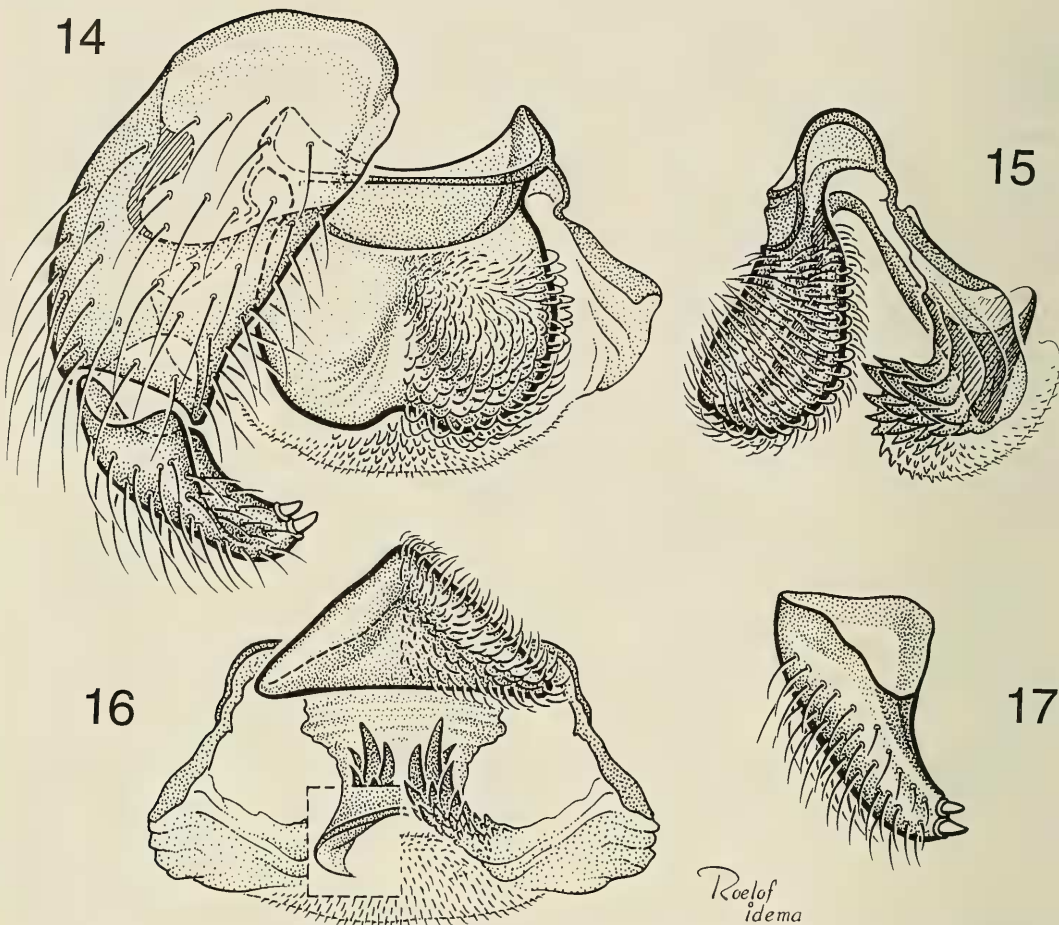
and at end of short neck. Median proximal space of cibarium broadly U-shaped, lacking setae or armature. Postpronotum light brown, with golden pile. Proepisternum light brown, with tuft of long golden setae. Scutum bright orange, with purple-brown border from lateral of midline to superalar region; anterior portion of this border extended posteriorly as a pair of thin, longitudinal stripes extended to scutellum; between this pair of stripes is a median stripe of similar color that also reaches posterior declivity; scutum clothed in decumbent golden pile, with posteriormost portion also with long golden brown recumbent setae.

Anepisternum and katepisternum yellowish orange; membranous regions pale brown. Region anterior of mesothoracic spiracle purple brown. Mesepimeral tuft golden brown. Mesbasisternum yellowish orange, rimmed in purple brown. Scutellum beige, with long, golden-brown setae, these being recumbent anteriorly and decumbent posteriorly. Metanotum dull orange brown, anterior 1/3 shiny brass brown. Wing translucent. Veins pale brown. Setae of stem vein and all other veins dark brown. Costa (C) with simple setae proximal to and simple setae and spinelike setae distal to about midpoint of subcosta (Sc). Sc haired ventrally. R_1 with one or two rows of setae, spinules present but not numerous, beginning apical to level of insertion of Sc with C. Rs simple, without any trace of forking. False vein forked apically. M_1 and M_2 nearly straight, reaching wing margin. CuA_1 and CuA_2 straight, reaching wing margin. A_1 straight, nearly reaching wing margin. A_2 strongly curved, not nearly reaching wing margin. Halter whitish, slightly tinged with brown, especially on capitulum. Legs yellow brown, with golden-brown, simple setae. Procoxa brown. Probasitarsus 13 times as long as wide. Mesocoxa and metacoxa yellowish orange. Metafemur with apex brown. Metatibia with base and apex brown. Metabasitarsus 7.5 times as long as wide. Calcipala rounded, extended to center of second tarsomere. Pedisulcus a series of shallow wrinkles along slightly concave surface of second tarsomere. Basal tooth of claw (Fig. 11) triangular, about 1/4 as long as claw. Abdominal tergites piceous, orange brown, with golden pile center of tergites pale brown, with posterior margin clothed with golden pile interspersed with sparse, brown pile. Membranous areas gray. Sternites orange brown with golden pile. Abdominal fringe beige, with long golden setae. Terminalia (Figs. 12–13) weakly sclerotized. Genital fork with stem expanded apically, arms expanded distally, and with long angled, dorsomedially projected apodemes. Ovipositor flaps broadly rounded

and with numerous setae. Spermatheca spherical, brown, moderately sclerotized, lacking noticeable sculpturing, and with distinct neck at junction with spermathecal duct. Anal lobe subquadrate, with somewhat prominent rounded lobe ventrally. Cercus flat, rounded posteriorly, the sclerotized apical portion about twice as tall as wide.

Male.—Thorax length 1.1–1.2 ($x = 1.2$, $n = 2$) mm. Wing length 3.1–3.2 ($x = 3.1$, $n = 2$) mm. Identical to that of female except as noted. Clypeus reduced to a narrow strip, with long brown pile. Sensory vesicle subglobular, with distinct neck, 0.4 times length of palpomere. Scutum with dark brown recumbent setae posteriorly. Procoxa yellowish orange. Wing much as in female, except spines on C beginning near junction of $R_1 + Rs$ and spines of R_1 beginning at junction of C and Sc. Scutellum shiny brass brown, with long dark-brown setae. Protarsus brown. Probasitarsus 8.5 times as long as wide. Meta basitarsus 5.3 times as long as wide. Abdominal tergites and sternites brown with anterior and posterior margins paler brown; membranous regions gray. Terminalia (Figs. 14–17) weakly sclerotized. Gonocoxite about three times longer than greatest width. Gonostylus about two-thirds as long as basimere, with two apical spines. Ventral plate about as wide as long, with median carina, and characteristic horizontal bridge connecting anterior arms. Median sclerite forked, the tines about 1/3 length of structure. Paramere weakly sclerotized distally, apex membranous and armed with approximately 12 large spines and several additional spines progressively smaller proximally.

Types.—Holotype: ♀ (pinned), USA: ARIZONA: Apache County, Government Spring, 50 m S of Forest Service Road 1120 (33°59'34"N, 109°27'54"W), elev. 8500 ft. (2591 m), 21 May 1994, J. K. Moulton (USNM). Paratypes: same data as holotype, except May 21–24 1994—8 larvae [4 Carnoy's (CNC), 4 absolute ethanol (JKM)], 1 pharate pupa (JKM), 7 pupae (2 each in



Figs. 14–17. *Gigantodax adleri*. 14, Male terminalia (ventral view with left gonocoxite and gonostylus removed). 15, Male ventral plate, median sclerite, and parameres (lateral view). 16, Male ventral plate, median sclerite, and parameres (terminal view). 17, Male right dististylus (dorsal view).

USNM and JKM, 1 each in CNC, NHM, and AMNH), and 4 pinned ♀s (1 each in CNC and NHM, 2 in JKM); same data, except 10 October 1994—10 larvae [5 Carnoy's (NHM), 5 absolute ethanol (JKM)]. Unnamed rivulet-like spring ca. 400 m S of Government Spring, 18 May 1994, J. K. Moulton—6 larvae (Carnoy's) and 1 pharate ♂ (in ethanol) (JKM). Small spring (seep) ca. 100 m N of Government Spring, 18 May 1994, J. K. Moulton—4 larvae (JKM). Graham County, Pinaleno Mountains, Twilight Spring @ Rt. 366, mile-marker 127 (32°40'47"N, 109°51'22"W), elev. ca. 7000 ft. (2134 m), 15 March 1995, J. K. Moul-

ton—1 larva (JKM). NEW MEXICO: Catron County, Fanny Spring @ Rt. 159 (Bursum Rd.) 4.2 km E of Mogollon (33°22'55"N, 108°45'59"W), elev. ca. 9000 ft (2744 m), 20 May 1995, J. K. Moulton—7 larvae, 1 pupa (NHM); same data, except 5 June 1995—4 larvae (NHM).

Etymology.—This remarkable species is named in honor of Peter H. Adler, a dear friend and mentor to whom I will be forever grateful for introducing me to the intriguing world of simuliids.

Diagnosis.—Female: The following suite of characters distinguishes this species from all others in the genus: (1) scutum bright

orange, bordered with purple brown, and clothed with golden-yellow pile; (2) setae of stem vein, legs, and scutellum dark golden brown; (3) mandible with 20 teeth along inner margin; (4) lacinia of maxilla with 18 teeth; (5) calcipala extended to 1/2 length of second tarsomere; and (6) basal tooth of claw small, triangular, about 1/5–1/4 as long as claw. Male: The bright orange, purple-brown bordered scutum clothed with golden pile, R_1 with spines, and dark brown stem vein and scutellar setae separate this species from all other species in the genus. Pupa: The five, flimsy, pale gray, tubelike filaments of the respiratory organ distinguishes this species from all others except *G. nasutus* Wygodzinsky and Coscarón. The gill of *G. adleri* differs from that of *G. nasutus* in the following regards: (1) filaments less stout, especially basally, not arising from a somewhat swollen gill base, (2) filaments directed more anterolaterally than anteriorly, and (3) second filament from dorsal and ventralmost filaments not strongly curved ventrally and dorsally, respectively, and pressed against the anterolateral portion of body. The protuberance of the frontoclypeus of *G. adleri* further distinguishes it from *G. nasutus* and possibly all other species. Larva: Larvae in this genus are not sufficiently characterized to make accurate species-level diagnoses without the presence of a respiratory histoblast. A preliminary analysis of larvae of several species indicates that those of many species are separable using nothing more than body coloration and pigment distribution if fixed in Carnoy's.

Remarks.—The preimaginal stages occur in springs approximately 0.1–1.0 m wide, a few cm deep, and less than 75 m in length. The temperature at the source of these springs is about 8–10°C, although during the day the temperature downstream may reach 15°C. The type locality, Government Spring, is the largest of three closely situated springs issuing from the western ridge of Lee Valley, just south of the town of Greer in the shadow of Baldy Peak (11,403

ft., 3477 m). Government Spring percolates at a modest rate through stones and herbaceous vegetation. The streambed is approximately 4 m in width, but the spring diverges such that any particular flow is only a few cm wide. The spring was once the water source for a Civilian Conservation Corps (CCC) trout hatchery (Peter Taylor—United States Forest Service, Apache-Sitgreaves Division, personal communication). Remnants of concrete pipes through which the spring is still partially diverted and six rectangular, trough-like, earthen holding tanks are clearly evident. Two other simuliids, *Simulium hechti* Vargas and Díaz Nájera and *S. patziciaense* Takaoka and Takahasi, belonging to the *Simulium hunteri* species-group were also found in the type locality. *Simulium patziciaense* was previously known only from Guatemala (Takaoka and Takahasi 1982). The dominant organism by far in the type locality was an *unidentified* species of amphipod.

The remaining two apparently unnamed springs near the type locality supported much smaller populations of both simuliids and amphipods. One is located approximately 400 m south of the type locality and is rivulet-like, with water flowing over large flat rocks and between large rocks and boulders. Located approximately 100 m north of Government Spring, the other spring is slow-flowing and has a mud bottom with few rocks and sparse vegetation. Associated with this new species in the rivulet was *Prosimulium travisi* Stone. No other simuliids were present in the mud-bottomed spring. The only other significant population of this species was found near the origin of Fanny Spring near the historic mining town of Mogollon, New Mexico. This spring is similar to the type locality in that it is well shaded and has watercress as the dominant herbaceous plant. Associated with this species in Fanny Spring were *S. patziciaense*, *S. piperi* Dyar and Shannon, and *S. puigi* Vargas, Martínez Palacios, and Díaz Nájera. *Simulium puigi* was previously known only from Chiapas, Oaxaca, Vera-

cruz, and Guatemala (Vargas et al. 1946, Takaoka and Takahasi 1982).

Larvae seem to prefer flat surfaces of rocks and the undersides of watercress leaves as substrates. Pupae were difficult to find at the type locality. Undoubtedly, the final instar larva moves into cracks and crevices of rocks or into filamentous algae to spin its flimsy cocoon, which becomes further obscured by the accumulation of debris. Of the two field-collected pupae, the one found at the type locality was in a clump of algae, and the one from Fanny Spring was on the underside of a watercress leaf. All laboratory-reared pupae were removed from crevices formed by parts of the stone bubbler assembly. Based upon the presence of numerous larvae of different size classes in both May and October, this species is presumably multivoltine. It is not known whether eggs or larvae overwinter.

The habitats described are potentially refugia, since they are inhabited by two species, *S. patziciaense* and *S. puigi*, previously known only from southern Mexico to Guatemala, and by *G. adleri*, whose closest relatives occur from southern Mexico to northern South America. On the other hand, these disparate distributions may be nothing more than an artifact resulting from a lack of faunistic research between these regions. Regardless, it is likely that additional species of *Gigantodax* occur in similar montaine habitats between southern Arizona and central Mexico.

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G. fulvescens (Blanchard) and *G. rufescens* (Edwards); and C. S. Chaboo (AMNH), for the loan of a paratype pupa of *G. nasutus*. This research was supported by D. R. Maddison and the NSF Research Training Group Grant in the Analysis of Biological Diversification (DIR-9113362) awarded to the University of Arizona.

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